Effects of blood parasite infections on spatiotemporal migration patterns and activity budgets in a long-distance migratory passerine

Tamara Emmenegger[1,2]*, Staffan Bensch[3], Steffen Hahn[1], Dmitry Kishkinev[4,5,6], Petr Procházka[7], Pavel Zehtindjiev[8], Silke Bauer[1]

[1] Department of Bird Migration, Swiss Ornithological Institute, Seerose 1, 6204 Sempach, Switzerland

[2] Institute of Integrative Biology, ETH Zurich, Rämistrasse 101, 8092 Zürich, Switzerland

[3] Molecular Ecology and Evolution Lab, Department of Biology, Lund University, Ecology Building, SE-22362 Lund, Sweden

[4] School of Natural Sciences, Bangor University, Bangor, Gwynedd, United Kingdom

[5] Biological Station Rybachy, Zoological Institute of Russian Academy of Sciences, 238535, Rybachy, Kaliningrad region, Russia

[6] School of Life Sciences, Keele University, Keele, Staffordshire, United Kingdom

[7] Institute of Vertebrate Biology, The Czech Academy of Sciences, Květná 8, CZ-60365 Brno, Czech Republic

[8] Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, 2 Yurii Gagarin Street, 1113 Sofia, Bulgaria

* tamara.emmenegger@vogelwarte.ch

Abstract

How blood parasite infections influence the migration of hosts remains a lively debated issue as past studies found negative, positive or no response to infections. This particularly applies to small birds, for which monitoring of detailed migration behaviour ovea whole annual cycle has been technically unachievable so far.

Here, we investigate how bird migration is influenced by parasite infections. To this end, we tracked great reed warblers (*Acrocephalus arundinaceus*) with multi-sensor loggers, characterized general migration patterns as well as detailed flight bout durations, resting times and flight heights and related these to the genus and intensity of their avian haemosporidian infections.

We found migration distances to be shorter and the onset of autumn migration to be delayed with increasing intensity of blood parasite infection, in particular for birds with *Plasmodium* and mixed-genus infections. Additionally, the durations of migratory flight bout were prolonged for infected compared to uninfected birds. But since severely infected birds and particularly birds with mixed genus infections had shorter resting times, initial delays seemed to be compensated for and the timing in other periods of the annual cycle was not compromised by infection.

Overall, our multi-sensor logger approach revealed that avian blood parasites have mostly subtle effects on migratory performance and that effects can occur in specific periods of the year only.

Keywords: activity, biologging, bird migration, flight height, great reed warbler, *Haemoproteus*, migration timing, parasites, *Plasmodium*, resting

Introduction

Infection-related deviations in host migration performance have already been described for a variety of parasite and host taxa: Monarch butterflies migrated slower when infected by ectoparasites (Bradley & Altizer, 2005), reindeer herds with more ectoparasites performed shorter migrations (Folstad, Nilssen, Halvorsen, & Andersen, 1991) and the timing of arrival at the breeding site was delayed for blood parasite infected compared to uninfected passerines (Rätti, Dufva, & Alatalo, 1993). A recent meta-analysis suggested movement capacity and phenology of migratory animals to be moderately affected by the status and intensity of infections, while body condition and survival were only weakly associated with infection (Risely, Klaassen, & Hoye, 2018). Nevertheless, the magnitude of parasite effects on migratory hosts and, particularly, how effects depend on the taxon and severity of infection, remain unresolved.

In migratory birds, parasites might affect host migration via several mechanistic pathways: Parasites could (i) directly reduce physiological performance and thereby lead to slower flight. Early seminal works indicated that *Plasmodium* infections decreased the oxygen consumption rates of experimentally infected canaries during nocturnal rest (Hayworth, Riper, & Weathers, 1987) and naturally infected lizards during exercise (Schall, Bennett, & Putnam, 1982). In contrast, the metabolic rates of a migratory passerine were not significantly influenced by infection neither during resting nor during exercise both for natural haemosporidian infections and experimental *Plasmodium* infections (Hahn et al., 2018).

Alternatively, parasites could (ii) indirectly impair host migration e.g. by slowing down fuelling, prolonging stopovers or increasing the need for resting after endurance flights. For instance, benign avian influenza infections lowered the feeding rates and prolonged stop-over durations in

migratory swans (van Gils et al., 2007) and infections with multiple intestinal parasites were correlated with delayed spring migration timing in passerines (López, Muñoz, Soriguer, & Figuerola, 2013).

Yet, regardless of the mechanisms behind parasite-effects on host migration, such changes are thought to cascade through to breeding, with delayed arrivals and late onset of breeding lowering individual fitness (Kokko, 199). However, so far, the insight into infection-related changes of host migration had been restricted to i) basic migration parameters measurable by standard methods (e.g. geolocation, telemetry and satellite tracking) and ii) snapshots of certain periods of the annual cycle. A full-migration approach relating detailed migration behaviour to individual infection parameters is still missing for wild birds.

Therefore, we used multisensor loggers to describe detailed migration patterns of great reed warblers (*Acrocephalus arundinaceus*) and related these patterns to the hosts' blood parasite infections (genera *Plasmodium* and *Haemoproteus* within Haemosporida). Multisensor loggers do not only enable geolocation by recording light, but also allow compiling individual activity and behaviour by recording accelero- and barometric data (Liechti et al., 2018). The recorded patterns were then related to the parasite genus and the individual intensities of avian haemosporidian parasite infections assessed by real-time quantitative PCR. Specifically, we related these infection parameters measured at the deployment and retrieval of the loggers to several key migration traits: distance, duration and speed of migration, the timing of autumn and spring migration, the duration of migratory flight bouts and resting periods, and flight height.

If infections affect migration throughout on a broad scale, we expect infected individuals to migrate shorter distances or to take longer for the same distance. If migration distance would vary

for infections with different parasite genera, this could both signify a parasite effect on migration performance and a differential probability of getting infected with different parasites in various regions of the non-breeding range. Depending on how infections affects migration timing, we may expect the following outcomes: If blood parasites hamper the preparation for migration, we expect that infected individuals to depart with delays. If, in contrast, blood parasites affect the progression of migration, we rather expect arrivals to be delayed. By using multisensor loggers, we also expect insights into the mechanisms behind parasite on migration patterns on a finer scale: If blood parasites impair flight, we expect infected birds to fly slower and their migratory flight bouts to be shorter (if fuel is limiting) or longer (if infected birds compensate for slower flight). If, in turn, blood parasites impair fuelling rates or increase energy expenditure, infected individuals are expected to need longer resting times. Finally, if partial oxygen pressures experienced aloft are limiting for migrating birds, we expect infected individuals to fly at lower altitudes. All these potential effects are expected to increase with growing intensity of infection and are to some degree expected to differ between parasite genera, as *Haemoproteus* and *Plasmodium* infections are known to differ in their average pathogenicity and co-infections with several genera are known to be most virulent (Valkiūnas, 2005).

Material & Methods

Study species and field sites

We investigated great reed warblers (*Acrocephalus arundinaceus*) breeding at three study sites in Bulgaria (BG, Kalimok Biological Station**,** 44.00°N 26.45°E**),** in the Czech Republic (CZ, Mutěnice, 48.90°N, 17.05°E) and in western Russia (RU, Rybachy, 55.15°N, 20.85°E). Great reed warblers breed in reed beds along fresh or brackish standing water and spend the non-breeding season in

sub-Saharan Africa (Koleček et al., 2016 and Figure 1a). They often harbour haemosporidian parasites – a widespread group of blood parasites which are transmitted by dipteran vectors – and within the two genera *Plasmodium* and *Haemoproteus* 29 genetic lineages have been recorded for great reed warblers (MalAvi database; Bensch, Hellgren, & Pérez-Tris, 2009; accessed on the 13.06.2019). The two parasite genera and their lineages can greatly vary in their virulence. While many infections are benign, some infected hosts can show fatigue and lose appetite during the acute phase or rarely even die (Lapointe, Atkinson, & Samuel, 2012). Most avian blood parasites infections become chronic and the minor effects of chronic infections are known to accumulate, e.g. resulting in reduced life-time reproductive success in great reed warblers (Asghar, Hasselquist, & Bensch, 2011).

Additionally, we found the maximum, but not the mean, resting durations to be reduced by infection, suggesting that, regardless of infection status, migrating birds need a certain minimum recovery period between consecutive migratory flight bouts. But extensive stop-over periods can be shortened to compensate for delays – may they be caused by infections or other factors. This also implies that focussing on a single migration variable (e.g. the arrival at a stopover or breeding site) may be insufficient, as parasite effects on timing in one phase of the annual cycle can be compensated with adjustments in other phases. Whether these adjustments come with the draw-back of being more exposed to predators due to compensatory feeding activity or of continuing migration in worse condition as shorter resting times cannot be compensated by extended feeding, cannot be tested with our data set.

In conclusion, using multi-sensor loggers enabled to describe detailed patterns in individual migration behaviours and how infections with parasites affect these. We found that chronic

infections with avian blood parasites have diverse, but relatively weak effects on the migration performance of great reed warblers. Our results also indicate that birds can compensate some effects of parasites arising in certain periods of the annual cycle, which thus might not be detectable anymore in subsequent periods. This indicates that hosts can cope with a broad range of chronic infection intensities, maintaining most of their migratory capacity and thus also their potential for spreading parasites (Bauer & Hoye, 2014).

Authors' contributions

TE, SH and SBa developed the conceptual framework of this study. DK, PP and PZ organized the field work and took care of permissions for their study sites. TE, DK, PP and SH carried out the field work. TE and SBe planned and conducted the lab work. TE and SBa analysed the data and drafted the manuscript. All co-authors contrbuted to writing of the manuscript, approved the final version and declared not to have any competing interests.

Acknowledgements

We thank D. Dimitrov, K. Ivanova, M. Ilieva, C. Sjöholm, S. Peev and M. Marinov, M. Požgayová, J. Koleček, K. Sosnovcová, V. Brlík and M. Šulc as well as , I. Ishchenko, D. Leoke, A. Anashina and the staff of Biological station 'Rybachy' for their assistance during field work in Bulgaria, Czech Republic and Russia, respectively. We also thank Tianhao Zhao for performing some of the qPCRs and Fränzi Korner-Nievergelt for statistical advice. This is report Nr. 66 of the Biological Experimental Station 'Kalimok'. We thank the Swiss National Science Foundation (31003A_160265), the Czech Science Foundation (20-00648S), the Bulgarian Science Foundation (DN01/6) and the Leverhulme Trust (RPG-2013288) for the funding.

Data accessibility statement

The datasets analysed and generated for this study are available on Zenodo (raw logger data: 10.5281/zenodo.4017739; migration variables and infection data: 10.5281/zenodo.4022516).

References

Adamík, P., Emmenegger, T., Briedis, M., Gustafsson, L., Henshaw, I., Krist, M., … Hahn, S. (2016). Barrier crossing in small avian migrants: individual tracking reveals prolonged nocturnal flights into the day as a common migratory strategy. *Scientific Reports*, *6*(February), 21560. doi: 10.1038/srep21560

Arlt, D., Low, M., & Pärt, T. (2013). Effect of Geolocators on Migration and Subsequent Breeding Performance of a Long-Distance Passerine Migrant. *PLoS ONE*, *8*(12), e82316. doi: 10.1371/journal.pone.0082316

Asghar, M., Hasselquist, D., & Bensch, S. (2011). Are chronic avian haemosporidian infections costly in wild birds? *Journal of Avian Biology*, *42*(6), 530–537. doi: 10.1111/j.1600-048X.2011.05281.x

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1), 1–48. doi: 10.18637/jss.v067.i01

Bauer, S., & Hoye, B. J. (2014). Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science (New York, N.Y.)*, *344*(6179), 1242552. doi: 10.1126/science.1242552

Bensch, S., Hellgren, O., & Pérez-Tris, J. (2009). MalAvi: a public database of malaria parasites and related haemosporidians in avian hosts based on mitochondrial cytochrome b lineages. *Molecular Ecology Resources*, *9*(5), 1353–1358. doi: 10.1111/j.1755-0998.2009.02692.x

Bradley, C. A., & Altizer, S. M. (2005). Parasites hinder monarch butterfly flight: Implications for disease spread in migratory hosts. *Ecology Letters*, *8*(3), 290–300. doi: 10.1111/j.1461-0248.2005.00722.x

Emmenegger, T., Bauer, S., Hahn, S., Müller, S. B., Spina, F., & Jenni, L. (2018). Blood parasites prevalence of migrating passerines increases over the spring passage period. *Journal of Zoology*, *306*(1), 23–27. doi: 10.1111/jzo.12565

Fallon, S. M., Ricklefs, R. E., Swanson, B. L., & Bermingham, E. (2003). Detecting Avian Malaria : An Improved Polymerase Chain Reaction Diagnostic. *J. Parasitology*, *89*(5), 1044–1047.

Folstad, I., Nilssen, A. C. a. C., Halvorsen, O., & Andersen, J. (1991). Parasite avoidance: the cause of post-calving migrations in Rangifer? *Canadian Journal of Zoology*, *69*(9), 2423–2429. doi: 10.1139/z91-340

Gelman, A., & Su, Y.-S. (2016). arm: Data Analysis Using Regression and Multilevel/Hierarchical Models. - R package version 1.10-1. Retrieved from https://cran.r-project.org/package=arm

Hahn, S., Bauer, S., Dimitrov, D., Emmenegger, T., Ivanova, K., Zehtindjiev, P., & Buttemer, W. A. (2018). Low intensity blood parasite infections do not reduce the aerobic performance of migratory birds. *Proceedings of the Royal Society B*, *285*(1871), 20172307. doi: http://dx.doi.org/10.1098/rspb.2017.2307

Hasselquist, D., Östman, Ö., Waldenström, J., & Bensch, S. (2007). Temporal patterns of occurrence and transmission of the blood parasite Haemoproteus payevskyi in the great reed warbler Acrocephalus arundinaceus. *Journal of Ornithology*, *148*(4), 401–409. doi: 10.1007/s10336-007-0144-2

Hayworth, A. M., Riper, C. Van, & Weathers, W. W. (1987). Effects of Plasmodium relictum on the Metabolic Rate and Body Temperature in Canaries (Serinus canarius). *The Journal of Parasitology*, *73*(4), 850–853. doi: 10.2307/3282431

Hellgren, O., Waldenström, J., & Bensch, S. (2004). *A NEW PCR ASSAY FOR SIMULTANEOUS STUDIES OF LEUCOCYTOZOON , PLASMODIUM , AND HAEMOPROTEUS FROM AVIAN BLOOD A NEW PCR ASSAY FOR SIMULTANEOUS STUDIES OF LEUCOCYTOZOON ,*. *90*(4), 797–802.

Himmel, T., Harl, J., Pfanner, S., Nedorost, N., Nowotny, N., & Weissenböck, H. (2020). Haemosporidioses in wild Eurasian blackbirds (Turdus merula) and song thrushes (T. philomelos): An in situ hybridization study with emphasis on exo-erythrocytic parasite burden. *Malaria Journal*, *19*(1), 1–13. doi: 10.1186/s12936-020-3147-6

Ilgūnas, M., Bukauskaitė, D., Palinauskas, V., Iezhova, T. A., Dinhopl, N., Nedorost, N., … Valkiūnas, G. (2016). Mortality and pathology in birds due to Plasmodium (Giovannolaia) homocircumflexum infection, with emphasis on the exoerythrocytic development of avian malaria parasites. *Malaria Journal*, *15*, 256. doi: 10.1186/s12936-016-1310-x

Kokko, H. (1999). Competition for early arrival birds in migratory birds. *Journal of Animal Ecology*, *68*(5), 940–950. Retrieved from http://onlinelibrary.wiley.com/doi/10.1046/j.1365-2656.1999.00343.x/full

Koleček, J., Hahn, S., Emmenegger, T., & Procházka, P. (2018). Intra-tropical movements as a beneficial strategy for Palearctic migratory birds. *Royal Society Open Science*, *5*(1), 171675. doi: 10.1098/rsos.171675

Koleček, J., Procházka, P., El-Arabany, N., Tarka, M., Ilieva, M., Hahn, S., … Hansson, B. (2016). Cross-continental migratory connectivity and spatiotemporal migratory patterns in the great reed warbler. *Journal of Avian Biology*, *47*(6), 756–767. doi: 10.1111/jav.00929

Lapointe, D. A., Atkinson, C. T., & Samuel, M. D. (2012). Ecology and conservation biology of avian malaria. *Annals of the New York Academy of Sciences*, *1249*(1), 211–226. doi: 10.1111/j.1749-6632.2011.06431.x

Liechti, F., Bauer, S., Dhanjal-Adams, K. L., Emmenegger, T., Zehtindjiev, P., & Hahn, S. (2018). Miniaturized multi-sensor loggers provide new insight into year-round flight behaviour of small trans-Sahara avian migrants. *Movement Ecology*, *6*(1), 19. doi: 10.1186/s40462-018-0137-1

Lisovski, S., & Hahn, S. (2012). GeoLight - processing and analysing light-based geolocator data in R. *Methods in Ecology and Evolution*. doi: 10.1111/j.2041-210X.2012.00248.x

Lisovski, S., Hewson, C. M., Klaassen, R. H. G., Korner-Nievergelt, F., Kristensen, M. W., & Hahn, S. (2012). Geolocation by light: Accuracy and precision affected by environmental factors. *Methods in Ecology and Evolution*, *3*(3), 603–612. doi: 10.1111/j.2041-210X.2012.00185.x

López, G., Muñoz, J., Soriguer, R., & Figuerola, J. (2013). Increased Endoparasite Infection in Late-Arriving Individuals of a Trans-Saharan Passerine Migrant Bird. *PLoS ONE*, *8*(4), e61236. doi: 10.1371/journal.pone.0061236

R Core Team. (2019). *R: A Language and Environment for Statistical Computing*. Retrieved from https://www.r-project.org/

Rätti, O., Dufva, R., & Alatalo, R. V. (1993). Blood parasites and male fitness in the pied flycatcher. *Oecologia*, *96*(3), 410–414. doi: 10.1007/BF00317512

Risely, A., Klaassen, M., & Hoye, B. J. (2018). Migratory animals feel the cost of getting sick: A meta-analysis across species. *Journal of Animal Ecology*, *87*(1), 301–314. doi: 10.1111/1365-2656.12766

Schall, J. J., Bennett, A. F., & Putnam, R. W. (1982). Lizards infected with malaria: physiological and behavioral consequences. *Science*, *217*(4564), 1057–1059. doi: 10.1126/science.7112113

Stahel, W. A. (2017). logst: Started Logarithmic Transformation. Retrieved from https://rdrr.io/rforge/regr0/man/logst.html

Stull, R. (2017). *Practical Meteorology: An Algebra-based Survey of Atmospheric Science*. Retrieved from https://www.eoas.ubc.ca/books/Practical_Meteorology/

Valkiūnas, G. (2005). *Avian malaria parasites and other haemosporidia*. Retrieved from https://www.crcpress.com/Avian-Malaria-Parasites-and-other-Haemosporidia/Valkiunas/p/book/9780415300971

Valkiūnas, G., Bairlein, F., Iezhova, T. A., & Dolnik, O. V. (2004). Factors affecting the relapse of Haemoproteus belopolskyi infections and the parasitaemia of Trypanosoma spp. in a naturally infected European songbird, the blackcap, Sylvia atricapilla. *Parasitology Research*, *93*(November), 218–222. doi: 10.1007/s00436-004-1071-2

van Gils, J. A., Munster, V. J., Radersma, R., Liefhebber, D., Fouchier, R. A. M., & Klaassen, M. (2007). Hampered Foraging and Migratory Performance in Swans Infected with Low-Pathogenic Avian Influenza A Virus. *PLoS ONE*, *2*(1), e184. doi: 10.1371/journal.pone.0000184

Yohannes, E., Hansson, B., Lee, R. W., Waldenström, J., Westerdahl, H., Åkesson, M., … Bensch, S. (2008). Isotope signatures in winter moulted feathers predict malaria prevalence in a breeding avian host. *Oecologia*, *158*(2), 299–306. doi: 10.1007/s00442-008-1138-3

Figures

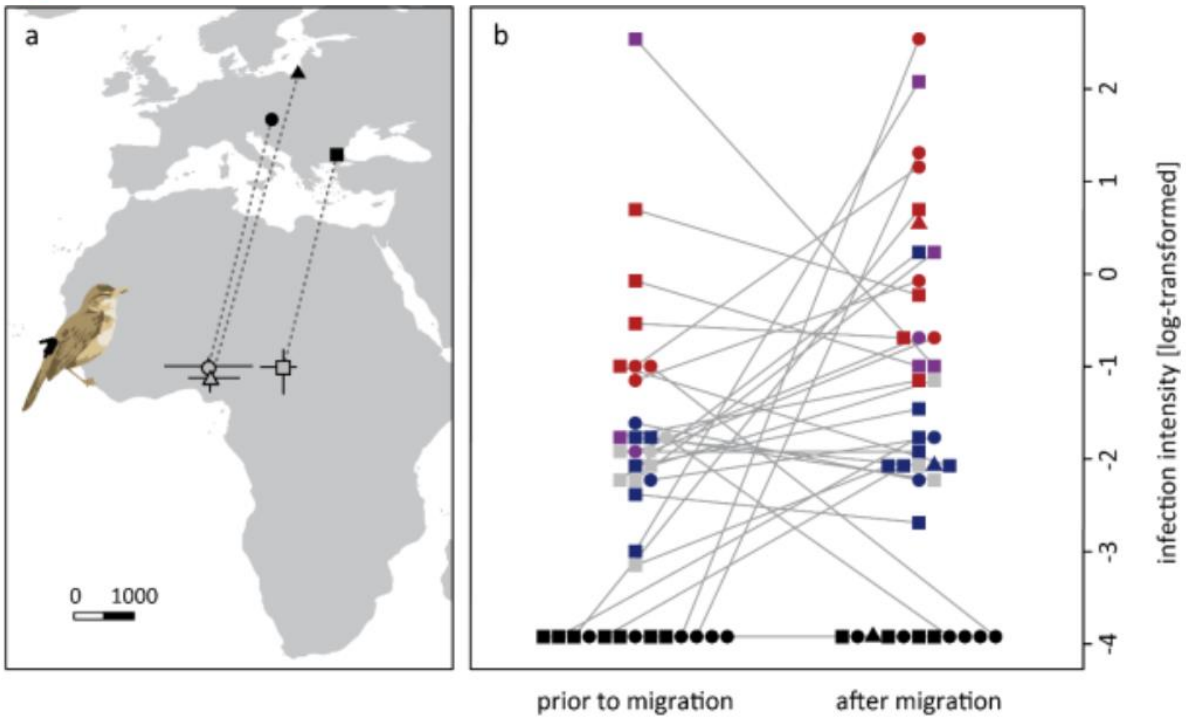

Figure 1: The breeding sites and site-specific non-breeding ranges of the tracked great reed warblers (a) as well as the individual genus and intensity of haemosporidian infections prior to and after the tracked migrations (b). Birds breeding in Bulgaria (closed square), Czech Republic (closed circle) and Russia (closed triangle) spent the non-breeding period in sub-Saharan Africa (open symbols = site-specific median, ± 25-75% quantiles of the individual non-breeding sites). The haemosporidian infections were generally more intense after than prior to the tracked migrations, and *Plasmodium* infections (blue) tended to be less intense than *Haemoproteus* infections (red) and mixed-genus infections (purple). Note that for some samples parasite genus is unknown (grey) and some points are unconnected as the pre-migration blood sample was missing (n = 3).

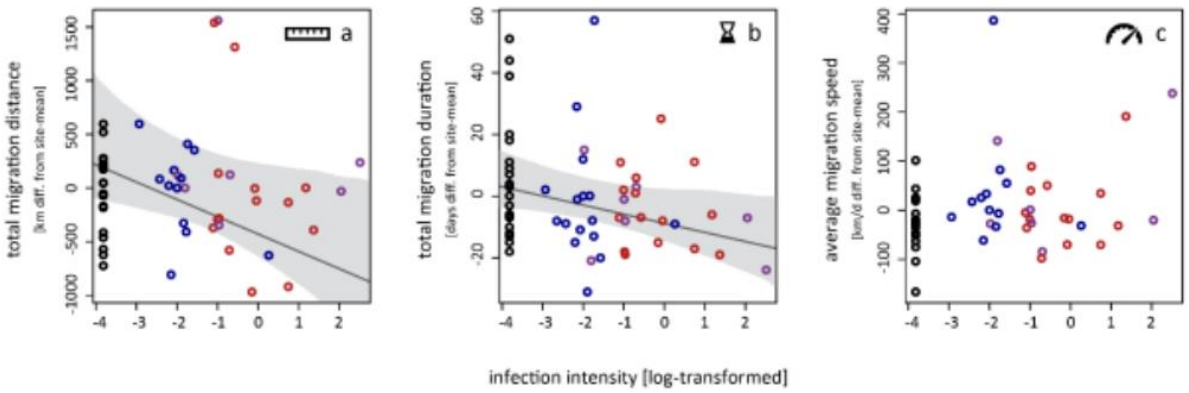

Figure 2: Effects of parasite infection on basic parameters of great reed warblers' migration. While the total migration distance (a) and the total migration duration (b) of infected great reed warblers were significantly related to the intensity, but not the genus (open symbols: Plasmodium = blue, Haemoproteus = red, mixed-genus = purple) of their haemosporidian infections, the resulting average migration speed (c) was statistically unrelated to both infection parameters.

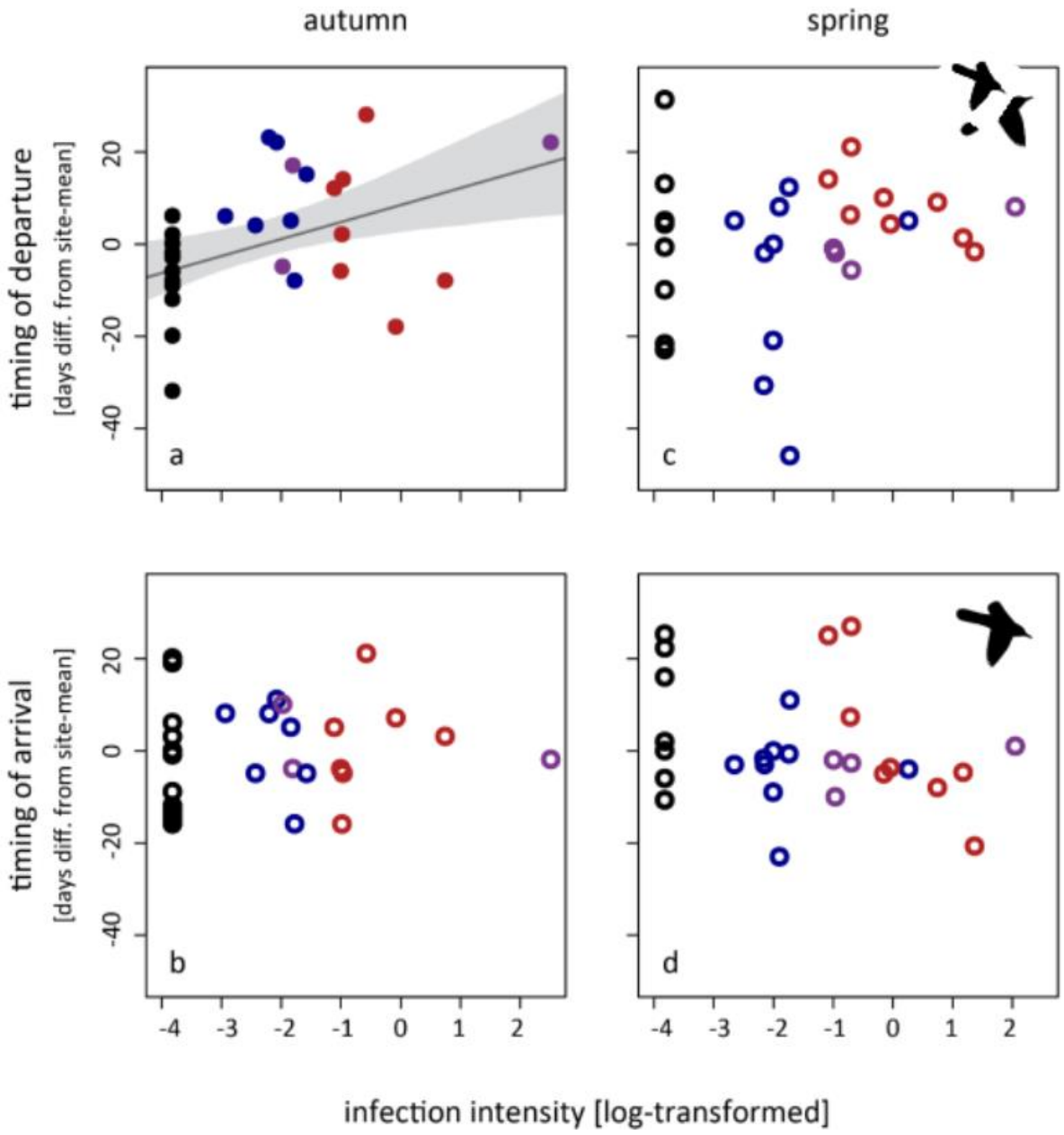

Figure 3: The timing of departures (a+c) and arrivals (b+d) of great reed warblers in autumn (a+b) and spring (c+d) as dependent on the haemosporidian infection. Only the departure for autumn migration was significantly related to genus (LM fit ± CrI; closed symbols: Plasmodium = blue, Haemoproteus = red, mixed-genus = purple) and intensity of infections. All other timing events were statistically unrelated to infection parameters (open symbols).

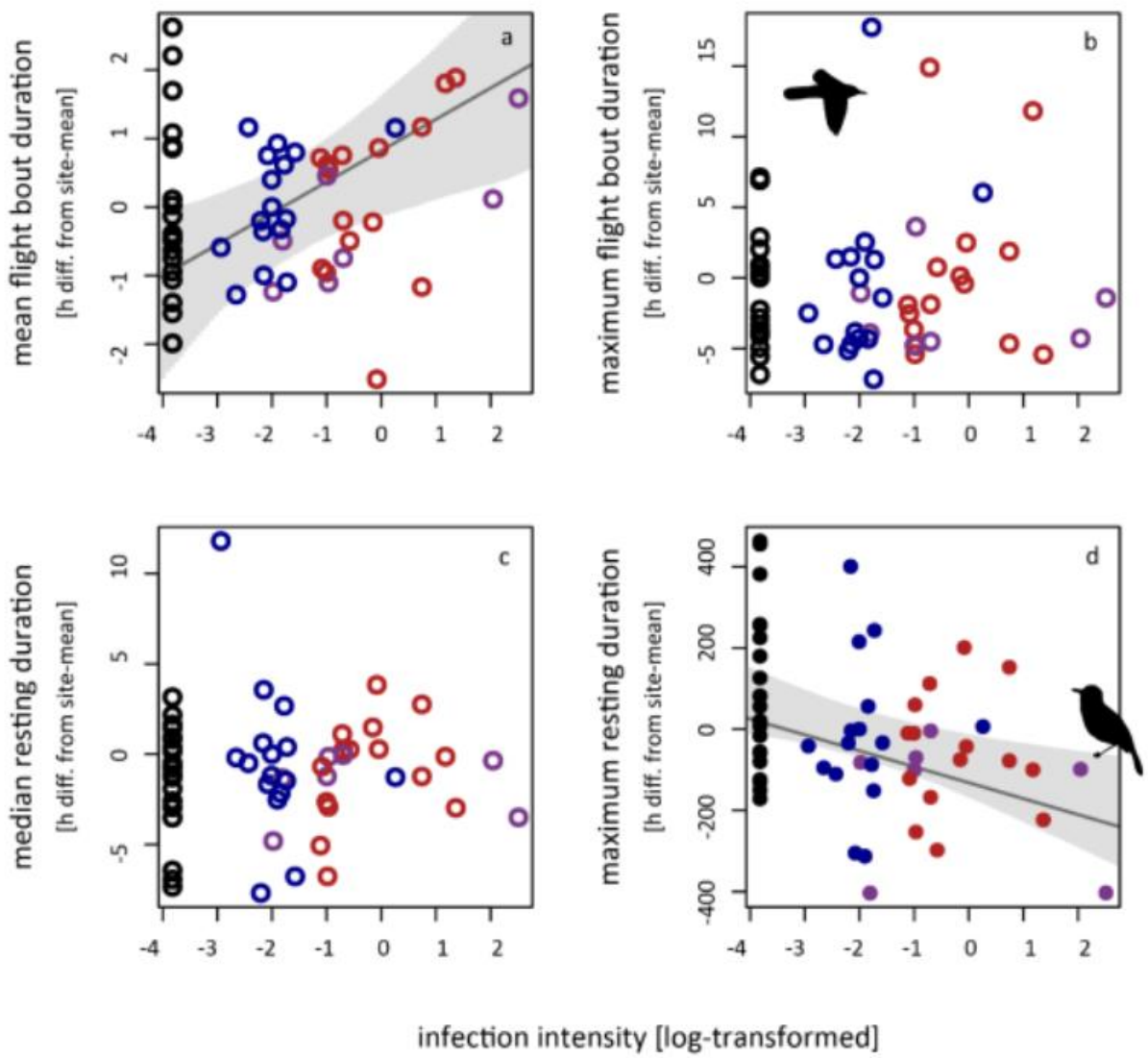

Figure 4: The interrelations between the haemosporidian infections of tagged great reed warbler with the mean (a) and the maximum (b) of individual flight bout durations as well as the median (c) and the maximum (d) individual resting durations. While mean flight times were merely related to infection intensity (LME fit ± CrI; open symbols: Plasmodium = blue, Haemoproteus = red, mixed-genus = purple), the maximal resting times were significantly related to both the intensity and the genus of the hosts' haemosporidian infections (LME fit ± CrI; closed symbols).

Appendix

Table S1: Overview on logger data and type of blood samples available from the tracked birds - sorted by logger ID.

general information				light data		multi-sensor data		blood smear		blood in SET	
logger id	ring id	study site	deployment year	autumn	spring	autumn	spring	before migration	after migration	before migration	after migration
14AZ	1-545764	bg	2015	1	1	1	1	1	0	0	0
14ES	1-545798	bg	2015	1	1	1	1	1	1	1	1
14FF	1-545865	bg	2015	1	1	1	1	1	1	1	1
14GD	1-545690	bg	2015	1	1	1	1	1	1	1	1
14GF	1-545842	bg	2015	1	1	1	1	1	1	1	1
14GG	1-545679	bg	2015	1	1	1	1	1	1	1	1
14GH	1-545683	bg	2015	1	1	1	1	1	1	1	1
14GS	1-545763	bg	2015	1	1	1	1	1	1	1	1
14GW	1-545859	bg	2015	0	0	1	1	1	1	1	1
14HA	1-545681	bg	2015	1	1	1	1	1	1	1	1
14HB	1-545703	bg	2015	1	0	1	0	1	1	1	1
14HC	1-545680	bg	2015	1	1	1	1	1	1	1	1
14HT	1-545817	bg	2015	1	0	1	0	1	1	1	1
14SD	za35988	cz	2016	1	1	1	1	1	1	1	1
14SF	za60716	cz	2016	1	1	1	1	1	1	1	1
14TC	za48338	cz	2016	1	1	1	1	1	1	1	1
14TF	za32371	cz	2016	1	0	1	0	1	1	1	1
14TS	1-545764	bg	2016	1	1	1	1	0	1	0	1
14TZ	1-545971	bg	2016	1	1	1	1	1	1	1	1
16BR	1-555140	bg	2016	1	1	1	1	1	1	1	1
16EA	fs27400	ru	2016	1	0	1	0	0	1	0	1
16ER	fs27378	ru	2016	1	1	1	1	0	1	0	1
16ET	fs27417	ru	2016	1	0	1	0	0	1	0	1
16EY	1-545791	bg	2016	1	1	1	1	1	1	1	1
16FB	1-545785	bg	2016	1	1	1	1	1	1	1	1
16FI	1-545777	bg	2016	1	1	1	1	1	1	1	1
16FT	1-545683	bg	2016	1	0	1	0	1	1	1	1
16GA	za59713	cz	2016	1	1	1	1	1	1	1	1

16HB	1-545761	bg	2016	1	1	1	1	1	1	1	1
16HL	1-545679	bg	2016	1	1	1	1	1	1	1	1
16HM	1-555134	bg	2016	1	1	1	1	1	1	1	1
18HA	ZA76610	cz	2017	1	0	1	0	1	1	1	1
18HY	ZA76621	cz	2017	1	1	1	1	1	1	1	1
18IC	ZA48339	cz	2017	1	1	1	1	1	1	1	1
18IJ	ZA69547	cz	2017	1	1	1	1	1	1	1	1
18IQ	ZA76620	cz	2017	1	0	1	0	1	1	1	1
18KA	ZA69517	cz	2017	1	1	1	1	1	1	1	1
18LD	ZA44432	cz	2017	1	1	1	1	1	1	1	1
18LX	ZA45656	cz	2017	1	1	1	1	1	1	1	1
18LZ	ZA62192	cz	2017	1	1	1	1	1	1	1	1

Table S2: The variables used in the models (also see Table S3). We list the abbreviations along with a full description, the units/levels and an annotation whether a variable was used as a response variable (RV), an explanatory variable (EV) or a random factor (RF).

Variable	Description	Unit/Levels	Used as?
am.start[1]	departure for autumn migration	day of the year	RV
am.end[1]	arrival from autumn migration	day of the year	RV
sm.star[1]	departure for spring migration	day of the year	RV
sm.end[1]	arrival from spring migration	day of the year	RV
dist[1]	total migration distance	kilometres	RV
migdur[1]	total migration duration	days	RV
speed[1]	total migration speed	kilometers/day	RV
durFB[2]	flight bout duration	hours	RV
durSO[2]	duration of resting period	hours	RV
FH[2]	flight height	meters a.s.l.	RV
int[3,4]	intensity of infection	relative qPCR intensity	EV
season	migration season	am = autumn sm = spring	EV
numSex	numerical sex of the host	1 = male 0 = female 0.5 = NA	EV
indi	individual geolocator id	40 different IDs	RF

[1] Unless stated otherwise, we centred this variable within study site by subtracting the site-specific mean from every individual value (indicated by the suffix '.pc').

[2] For this variable we calculated the mean, median, max and/or sum per individuum to be used in the models.

[3] This variable was used as unitless log-transformed values.

[4] We used 'int1' when we involved the intensity from the sample before to the tracked migration, 'int2' for the sample after or 'int' when we used either of the two samples.

Table S3: List of model formulas and parameter estimates from models with (A) parasite genus as the only focal explanatory variable, (B) parasite genus and infection intensity as two focal explanatory variables and (C) infection intensity as the only focal explanatory variable (from left to right), and the models with (1) basic migration parameters, (2) migration timing parameters, (3) flight times, (4) resting times and (5) flight heights as response variables (from top to the bottom). Significant estimates and the according variables are shown in bold. The suffix '.pc' indicates that a variable has been centred within each site by subtracting the site-specific mean from the individual values. See Table S2 for a glossary of the variables used in the models.

(A) GENUS ONLY	(B) LOGST(INT) + GENUS	(C) LOGST(INT) ONLY
(1) Basic migration parameters		
dist.pc ~ genus + season + Sex + (1 | indi) Fixed effects: Estimate Std. Error df t value Pr(>|t|) (Intercept) 185.55 183.49 35.76 1.011 0.319 genusP -34.00 201.62 42.64 -0.169 0.867 genusH -103.55 196.82 45.69 -0.526 0.601 genusHP -19.90 253.85 40.91 -0.078 0.938 seasonsm 57.61 133.69 16.42 0.431 0.672 Sex -264.32 187.62 25.04 -1.409 0.171	**dist.pc ~ logstint** + genus + season + Sex + (1 | indi) Fixed effects: Estimate Std. Error df t value Pr(>|t|) (Intercept) -429.20 358.41 31.65 -1.198 0.240 **logstint -161.38 76.82 19.26 -2.101 0.049 *** genusP 225.21 240.02 35.42 0.938 0.354 genusH 483.03 342.50 31.64 1.410 0.168 genusHP 391.16 375.69 38.04 1.041 0.304 seasonsm 149.67 122.05 12.89 1.226 0.242 Sex -269.40 192.06 25.04 -1.403 0.173	dist.pc ~ logstint + season + Sex + (1 | indi) Fixed effects: Estimate Std. Error df t value Pr(>|t|) (Intercept) 17.17 158.51 47.27 0.108 0.914 logstint -60.11 39.82 48.90 -1.509 0.138 seasonsm 97.22 114.88 26.37 0.846 0.405 Sex -240.66 170.52 36.74 -1.411 0.167
migdur.pc ~ genus + season + Sex + (1 | indi) Fixed effects: Estimate Std. Error df t value Pr(>|t|) (Intercept) 2.750 5.628 53.000 0.489 0.627 genusP -7.347 6.065 53.000 -1.212 0.231 genusH -9.089 6.362 53.000 -1.429 0.159 genusHP -11.889 7.947 53.000 -1.496 0.141 seasonsm 2.834 4.819 53.000 0.588 0.559 Sex 1.932 5.347 53.000 0.361 0.719	migdur.pc ~ logstint + genus + season + Sex + (1 | indi) Fixed effects: Estimate Std. Error df t value Pr(>|t|) (Intercept) -10.4884 13.2000 52.0000 -0.795 0.430 logstint -3.3509 3.0236 52.0000 -1.108 0.273 genusP -1.1984 8.2101 52.0000 -0.146 0.885 genusH 2.8344 12.4921 52.0000 0.227 0.821 genusHP -0.1707 13.2168 52.0000 -0.013 0.990 seasonsm 3.7986 4.8869 52.0000 0.777 0.440 Sex 2.0243 5.3358 52.0000 0.379 0.706	**migdur.pc ~ logstint** + season + Sex + (1 | indi) Fixed effects: Estimate Std. Error df t value Pr(>|t|) (Intercept) -9.242 4.829 65.000 -1.914 0.0601 . **logstint -2.768 1.337 65.000 -2.070 0.0424 *** seasonsm 1.744 4.251 65.000 0.410 0.6829 Sex 4.446 4.532 65.000 0.981 0.3302
speed.pc ~ genus + season + Sex + (1 | indi) Fixed effects: Estimate Std. Error df t value Pr(>|t|) (Intercept) -20.000 30.524 37.480 -0.655 0.5163 genusP 65.833 33.615 43.058 1.958 0.0567 . genusH 28.576 32.918 45.929 0.868 0.3899 genusHP 70.066 42.288 40.695 1.657 0.1052 seasonsm -9.820 22.614 19.435 -0.434 0.6689 Sex -3.886 31.103 27.587 -0.125 0.9015	speed.pc ~ logstint + genus + season + Sex + (1 | indi) Fixed effects: Estimate Std. Error df t value Pr(>|t|) (Intercept) 58.9324 63.1840 37.0601 0.933 0.357 logstint 19.8273 13.8971 26.7744 1.427 0.165 genusP 29.8258 41.9806 40.4443 0.710 0.481 genusH -43.6364 60.2706 38.4840 -0.724 0.473 genusHP 0.6138 65.1513 44.0144 0.009 0.993 seasonsm -17.4979 22.6579 17.2428 -0.772 0.450 Sex -5.0208 31.0972 26.5386 -0.161 0.873	speed.pc ~ logstint + season + Sex + (1 | indi) Fixed effects: Estimate Std. Error df t value Pr(>|t|) (Intercept) 28.398 24.590 55.000 1.155 0.2531 logstint 12.870 6.855 55.000 1.878 0.0658 . seasonsm -11.601 23.552 55.000 -0.493 0.6243 Sex 1.349 24.877 55.000 0.054 0.9569
(2) Migration timing		
am.start.pc ~ genus1 + numSex Coefficients: Estimate Std. Error t value Pr(>|t|) (Intercept) -2.700 4.390 -0.615 0.54414 **genus1P 16.773 5.475 3.064 0.00518 **** genus1H 10.088 5.507 1.832 0.07889 . **genus1HP 19.271 7.463 2.582 0.01606 *** numSex -7.699 4.544 -1.694 0.10268	am.start.pc ~ logstint1 + genus1 + numSex Coefficients: Estimate Std. Error t value Pr(>|t|) (Intercept) 4.093 12.250 0.334 0.7412 logstint1 1.719 2.888 0.595 0.5573 genus1P 13.821 7.441 1.857 0.0756 . genus1H 4.447 11.000 0.404 0.6896 genus1HP 13.437 12.380 1.085 0.2885 numSex -8.042 4.640 -1.733 0.0959 .	**am.start.pc ~ logstint1** + numSex Coefficients: Estimate Std. Error t value Pr(>|t|) (Intercept) 13.574 4.308 3.151 0.00339 ** **logstint1 3.638 1.271 2.863 0.00713 **** numSex -8.040 4.041 -1.990 0.05471 .
am.end.pc ~ genus1 + numSex Coefficients: Estimate Std. Error t value Pr(>|t|) (Intercept) -2.0701 4.3200 -0.479 0.636 genus1P 3.3621 5.3878 0.624 0.538 genus1H 4.0383 5.4190 0.745 0.463 genus1HP 3.8818 7.3441 0.529 0.602 numSex -0.4723 4.4721 -0.106 0.917	am.end.pc ~ logstint1 + genus1 + numSex Coefficients: Estimate Std. Error t value Pr(>|t|) (Intercept) -4.9882 12.1262 -0.411 0.684 logstint1 -0.7384 2.8590 -0.258 0.798 genus1P 4.6302 7.3663 0.629 0.536 genus1H 6.4619 10.8890 0.593 0.558 genus1HP 6.3881 12.2556 0.521 0.607 numSex -0.3248 4.5936 -0.071 0.944	am.end.pc ~ logstint1 + numSex Coefficients: Estimate Std. Error t value Pr(>|t|) (Intercept) 2.4280 3.9642 0.612 0.544 logstint1 0.9252 1.1691 0.791 0.434 numSex -0.4663 3.7178 -0.125 0.901
sm.start.pc ~ genus2 + numSex Coefficients: Estimate Std. Error t value Pr(>|t|) (Intercept) -0.141603 8.245046 -0.017 0.986 genus2P -7.486973 7.699201 -0.972 0.341 genus2H 8.249150 8.548787 0.965 0.344 genus2HP 0.058969 9.687533 0.006 0.995 numSex -0.001944 7.463227 0.000 1.000	sm.start.pc ~ logstint2 + genus2 + numSex Coefficients: Estimate Std. Error t value Pr(>|t|) (Intercept) 1.5097 16.5168 0.091 0.928 logstint2 0.4460 3.8374 0.116 0.908 genus2P -8.3990 11.1090 -0.756 0.457 genus2H 6.5409 17.0961 0.383 0.706 genus2HP -1.5728 17.1764 -0.092 0.928 numSex 0.0631 7.6420 0.008 0.993	sm.start.pc ~ logstint2 + numSex Coefficients: Estimate Std. Error t value Pr(>|t|) (Intercept) 7.4491 5.4190 1.375 0.180 logstint2 0.8066 1.8205 0.443 0.661 numSex -9.1303 6.5896 -1.386 0.176
sm.end.pc ~ genus2 + numSex Coefficients: Estimate Std. Error t value Pr(>|t|) (Intercept) 11.809 6.550 1.803 0.084 . genus2P -7.840 6.117 -1.282 0.212 genus2H -6.382 6.791 -0.940 0.357 genus2HP -8.740 7.696 -1.136 0.267 numSex -8.587 5.929 -1.448 0.160	sm.end.pc ~ logstint2 + genus2 + numSex Coefficients: Estimate Std. Error t value Pr(>|t|) (Intercept) -5.355 12.449 -0.430 0.671 logstint2 -4.635 2.892 -1.603 0.123 genus2P 1.640 8.373 0.196 0.846 genus2H 11.374 12.885 0.883 0.387 genus2HP 8.221 12.946 0.635 0.532 numSex -9.263 5.760 -1.608 0.121	sm.end.pc ~ logstint2 + numSex Coefficients: Estimate Std. Error t value Pr(>|t|) (Intercept) 2.075 3.782 0.549 0.5875 logstint2 -2.307 1.271 -1.816 0.0797 . numSex -8.685 4.599 -1.888 0.0690 .
(3) Flight times		
durFB.mean.pc ~ genus + season + Sex + (1 | indi) Fixed effects:	**durFB.mean.pc ~ logstint** + genus + season + Sex + (1 | indi) Fixed effects:	durFB.mean.pc ~ logstint + season + Sex + (1 | indi) Fixed effects:

```
             Estimate Std. Error       df t value Pr(>|t|)
(Intercept)  0.02460    0.37246 41.24017   0.066    0.948
genusP       0.18642    0.39433 47.90401   0.473    0.639
genusH       0.19681    0.41069 50.58490   0.479    0.634
genusHP      0.08910    0.52795 44.05214   0.169    0.867
seasonsm    -0.01743    0.27265 30.32173  -0.064    0.949
Sex         -0.24174    0.36617 31.83505  -0.660    0.514
```

```
             Estimate Std. Error       df t value Pr(>|t|)
(Intercept)  1.8224     0.7821 51.6456   2.330    0.0237 *
logstint     0.4560     0.1768 47.7811   2.579    0.0130 *
genusP      -0.6323     0.4910 51.8964  -1.288    0.2036
genusH      -1.4318     0.7440 51.9922  -1.924    0.0598 .
genusHP     -1.5806     0.7969 50.6513  -1.983    0.0528 .
seasonsm    -0.1375     0.2739 29.9640  -0.502    0.6193
Sex         -0.2527     0.3366 29.9887  -0.751    0.4587
```

```
             Estimate Std. Error       df t value Pr(>|t|)
(Intercept)  0.57640    0.35342 53.21645   1.631    0.109
logstint     0.13786    0.09454 64.87535   1.458    0.150
seasonsm    -0.10354    0.26659 36.09857  -0.388    0.700
Sex         -0.39837    0.34961 35.73147  -1.139    0.262
```

```
durFB.max.pc ~ genus + season + Sex + (1 | indi)

Fixed effects:
             Estimate Std. Error       df t value Pr(>|t|)
(Intercept)  -1.9448     1.7410 32.3423  -1.117    0.272
genusP        0.1341     1.8420 42.9742   0.073    0.942
genusH        0.9023     1.9177 48.1383   0.471    0.640
genusHP      -1.6268     2.4671 36.7901  -0.659    0.514
seasonsm      0.6623     1.2685 19.7072   0.522    0.607
Sex           1.6716     1.7133 21.3003   0.976    0.340
```

```
durFB.max.pc ~ logstint + genus + season + Sex + (1 | indi)

Fixed effects:
             Estimate Std. Error       df t value Pr(>|t|)
(Intercept)  1.3160     3.8155 49.8441   0.345    0.732
logstint     0.8203     0.8535 39.6182   0.961    0.342
genusP      -1.3539     2.4088 51.8865  -0.562    0.577
genusH      -2.0712     3.6407 51.2685  -0.569    0.572
genusHP     -4.5628     3.9306 51.2861  -1.161    0.251
seasonsm     0.4340     1.2904 19.9101   0.336    0.740
Sex          1.6329     1.7162 21.7179   0.951    0.352
```

```
durFB.max.pc ~ logstint + season + Sex + (1 | indi)

Fixed effects:
             Estimate Std. Error       df t value Pr(>|t|)
(Intercept)  -0.2280     1.6748 52.8694  -0.136    0.892
logstint      0.2991     0.4233 63.1852   0.707    0.482
seasonsm     -0.3032     1.0928 35.6097  -0.277    0.783
Sex           1.4059     1.7303 37.0539   0.813    0.422
```

(4) Resting times

```
durSO.mean.pc ~ genus + season + Sex + (1 | indi)
Fixed effects:
             Estimate Std. Error       df t value Pr(>|t|)
(Intercept)  -1.1759     1.0067 38.3077  -1.168   0.2500
genusP        0.8055     1.0702 45.6124   0.753   0.4555
genusH       -0.1134     1.1170 48.6977  -0.102   0.9196
genusHP      -1.1809     1.4288 39.8855  -0.827   0.4134
seasonsm      2.0587     0.7587 27.0921   2.713   0.0114 *
Sex          -1.3849     0.9839 27.9010  -1.408   0.1703
```

```
durSO.mean.pc ~ logstint + genus + season + Sex + (1 | indi)

Fixed effects:
             Estimate Std. Error       df t value Pr(>|t|)
(Intercept) -2.64016    2.24882 51.08715  -1.174  0.24583
logstint    -0.36713    0.50526 45.14071  -0.727  0.47121
genusP       1.48508    1.41670 51.99960   1.048  0.29937
genusH       1.21676    2.14326 51.80493   0.568  0.57268
genusHP      0.08963    2.30678 51.19049   0.039  0.96916
seasonsm     2.15952    0.77110 26.99632   2.801  0.00931 **
Sex         -1.35880    0.99371 28.14858  -1.367  0.18232
```

```
durSO.mean.pc ~ logstint + season + Sex + (1 | indi)

Fixed effects:
             Estimate Std. Error       df t value Pr(>|t|)
(Intercept)  -1.4658     0.8462 52.6913  -1.732   0.0891 .
logstint     -0.1456     0.2325 61.0186  -0.626   0.5335
seasonsm      1.9585     0.7202 35.7824   2.719   0.0100 *
Sex          -1.0992     0.8075 33.8499  -1.361   0.1825
```

```
durSO.max.pc ~ genus + season + Sex + (1 | indi)

Fixed effects:
             Estimate Std. Error       df t value Pr(>|t|)
(Intercept)    22.67      58.24    39.56   0.389  0.69918
genusP       -118.92      61.45    47.55  -1.935  0.05893 .
genusH       -116.58      63.88    50.82  -1.825  0.07391 .
genusHP      -268.92      82.42    43.91  -3.263  0.00214 **
seasonsm       34.31      41.70    27.50   0.823  0.41773
Sex            70.33      57.51    29.60   1.223  0.23100
```

```
durSO.max.pc ~ logstint + genus + season + Sex + (1 | indi)

Fixed effects:
             Estimate Std. Error       df t value Pr(>|t|)
(Intercept)   -54.24     127.07    50.41  -0.427    0.671
logstint      -19.28      28.32    43.08  -0.681    0.500
genusP        -84.16      80.35    51.80  -1.047    0.300
genusH        -45.95     121.36    51.33  -0.379    0.707
genusHP      -199.84     131.34    51.81  -1.521    0.134
seasonsm       39.42      42.50    26.70   0.927    0.362
Sex            71.67      58.00    29.15   1.236    0.226
```

```
durSO.max.pc ~ logstint + season + Sex + (1 | indi)

Fixed effects:
             Estimate Std. Error       df t value Pr(>|t|)
(Intercept)  -131.79      49.14    52.97  -2.682  0.00974
**
logstint      -39.24      13.38    63.57  -2.932  0.00467
**
seasonsm       23.23      39.58    35.68   0.587  0.56089
Sex            63.98      47.57    34.40   1.345  0.18748
```

(5) Flight height

```
FH.mean.pc ~ genus + season + Sex + (1 | indi)

Fixed effects:
             Estimate Std. Error       df t value Pr(>|t|)
(Intercept)  -107.18      103.63   42.36  -1.034    0.307
genusP        128.20      106.30   51.43   1.206    0.233
genusH        190.87      108.74   52.99   1.755    0.085 .
genusHP       126.45      143.27   51.61   0.883    0.382
seasonsm       -2.10       64.00   27.89  -0.033    0.974
Sex            26.08      105.28   33.16   0.248    0.806
```

```
FH.mean.pc ~ logstint + genus + season + Sex + (1 | indi)

Fixed effects:
             Estimate Std. Error       df t value Pr(>|t|)
(Intercept)   228.77     206.99    49.28   1.105   0.2744
logstint       82.46      45.42    40.13   1.816   0.0769 .
genusP        -32.43     131.59    50.86  -0.246   0.8063
genusH       -119.88     198.24    50.14  -0.605   0.5481
genusHP      -183.91     216.41    51.92  -0.850   0.3993
seasonsm      -24.89      66.48    26.43  -0.374   0.7111
Sex            20.67      99.91    30.85   0.207   0.8375
```

```
FH.mean.pc ~ logstint + season + Sex + (1 | indi)

Fixed effects:
             Estimate Std. Error       df t value Pr(>|t|)
(Intercept)   104.16      84.57    51.44   1.232  0.22370
logstint       56.93      21.16    62.21   2.691  0.00915
**
seasonsm      -25.94      54.03    33.43  -0.480  0.63427
Sex            40.98      87.88    35.13   0.466  0.64392
```

```
FH.max.pc ~ genus + season + Sex + (1 | indi)

Fixed effects:
             Estimate Std. Error       df t value Pr(>|t|)
(Intercept)    94.94     297.38    36.03   0.319    0.751
genusP       -544.89     312.65    46.40  -1.743    0.088 .
genusH       -193.21     324.40    50.84  -0.596    0.554
genusHP      -273.62     419.99    42.68  -0.651    0.518
seasonsm      204.82     208.28    22.67   0.983    0.336
Sex            47.29     294.93    25.29   0.160    0.874
```

```
FH.max.pc ~ logstint + genus + season + Sex + (1 | indi)

Fixed effects:
             Estimate Std. Error       df t value Pr(>|t|)
(Intercept)  1115.66     639.66    51.78   1.744   0.0871 .
logstint      236.06     145.30    46.72   1.625   0.1110
genusP      -1142.93     400.39    51.31  -2.855   0.0062 **
genusH      -1117.70     607.47    51.94  -1.840   0.0715 .
genusHP     -1250.35     648.05    48.27  -1.929   0.0596 .
seasonsm      117.63     228.09    22.43   0.516   0.6111
Sex            42.39     269.50    21.52   0.157   0.8765
```

```
FH.max.pc ~ logstint + season + Sex + (1 | indi)

Fixed effects:
             Estimate Std. Error       df t value Pr(>|t|)
(Intercept)   -20.10     279.78   51.00  -0.072    0.943
logstint       13.01      70.60   62.73   0.184    0.854
seasonsm       42.11     181.96   32.71   0.231    0.818
Sex            75.81     289.30   34.21   0.262    0.795
```

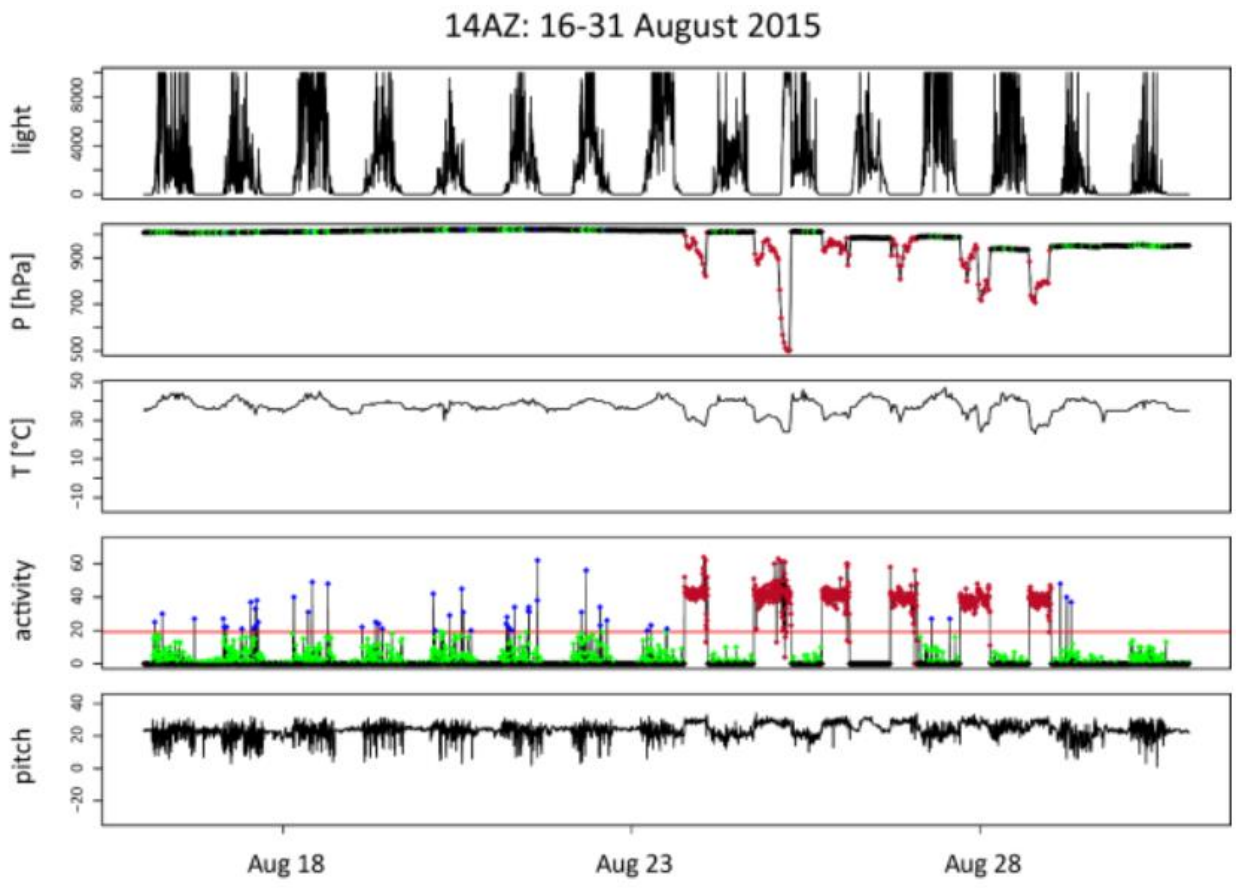

Figure S1: A sample data set for the period 16-31 August 2015 from a great reed warbler with the multi-sensor logger ID 14AZ. The panels depict data from the different sensors (from top to the bottom): light intensity, air pressure, ambient temperature, locomotor activity and pitch (i.e. mean body position). The colours in the pressure and activity panels show behaviours categorised as 'resting' (black), 'active' (green), 'flight' (blue) and 'migratory flight' (red).